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COMBINED EFFECTS OF SALINITY AND TEMPERATURE ON THE FEEDING, REPRODUCTIVE, AND SURVIVAL RATES OF *EUPLEURA CAUDATA* (SAY) AND *UROSALPINX CINEREA* (SAY) (PROSOBRANCHIA: MURICIDAE)[1]

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The marine prosobranch gastropods, *Eupleura caudata* (Say) and *Urosalpinx cinerea* (Say), are among the most serious predators of the Eastern oyster (*Crassostrea virginica*). The damage inflicted by these drills is estimated to be in the millions of dollars per year (Nelson, 1931; Galtsoff, Prytherch, and Engle, 1937). Both species are widely distributed along the coastal waters of the eastern United States, often inhabiting areas where salinity and temperature vary with seasonal and tidal cycles. The natural exposure of these gastropods to a fluctuating environment has led investigators to study the influence of salinity or temperature on their physiological activities.

Many investigators believed that drills begin to feed only above a certain critical temperature (Federighi, 1931a; Galtsoff *et al.*, 1937; Cole, 1942; Adams, 1947; Hancock, 1954). After the proposal of physiological speciation in oyster drills (Stauber, 1950; Loosanoff and Davis, 1951), however, many authorities accepted the suggestion that no one critical temperature exists at which all oyster drills begin feeding (Hanks, 1957; Franz, 1966). The effect of salinity on feeding rates of oyster drills has been investigated only superficially in field studies (Haskin, 1935; Sizer, 1936).

The initiation and rate of egg capsule deposition appear to be greatly influenced by temperature (Federighi, 1931a; Cole, 1942; Hancock, 1959; Franz, 1966, 1967), although other factors, such as food, availability of suitable substratum, and population density, may be contributory regulators of spawning intensity (Stauber, 1943; Carriker, 1955; Galtsoff *et al.*, 1937). Loosanoff and Davis (1951) reported that a single species-wide critical temperature for egg capsule deposition does not exist for *U. cinerea*. This situation could be expected from populations collected from different geographical areas but it also appears to hold true among populations collected from the same area. The effect of salinity on egg capsule deposition has been less thoroughly investigated, although available reports suggest that salinity is a regulator of spawning activities of drills (Federighi, 1931a; Stauber, 1943; Carriker, 1955).

Oyster drills appear to remain active over a relatively wide temperature range (Sizer, 1936; Hanks, 1957); however, the effect of salinity on drill survival is

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relatively unknown. Many reports on the effect of salinity on oyster drills are conflicting, particularly concerning the minimum salinity at which the drills can survive (Federighi, 1931b; Sizer, 1936; Griffith and Engle, 1962).

Sizer (1936), on the basis of his experimental results, concluded that *U. cinerea* are active only between 20 and 30‰. Galtsoff *et al.* (1937) found drills active in Delaware Bay between 15 and 29‰ at summer temperatures. Stauber (1943) concluded, from field observations and laboratory experiments, that *U. cinerea* remain active over a fairly wide salinity range and that they can move in salinities as low as 8‰ at low winter temperatures.

Many of the conclusions concerning the effects of temperature and salinity on oyster drills are conflicting. Although differences in individual experimental procedures and differences in test populations attributable to physiological speciation may account for some of these disparities, it is now evident that the effects of salinity and temperature cannot be analyzed by monofactorial experiments. Kinne (1964) recognized that monofactorial experiments on the effects of a single environmental variable may yield results that are ecologically invalid. He suggested that a polyfactorial approach be used whenever possible to analyze the influence of environmental stimuli.

Data are scant on the combined effects of two environmental stimuli on oyster drills. Stauber (1943), who was the first to evaluate the influence of temperature on the response of oyster drills to salinity, concluded that the survival of drills exposed to low salinities increased as the temperature was lowered and decreased as the temperature was increased. More recently, the combined effect of temperature and salinity on larval stages was determined for *C. virginica* and *Mercenaria mercenaria* (Davis and Calabrese, 1964) and for *Mulinia lateralis* (Calabrese, 1969). They concluded that the effects of these environmental factors were interrelated; changes of either factor influenced the effect of the other. The present bifactorial investigation was initiated to determine the combined effect of salinity and temperature on the feeding, reproduction, and survival of the two oyster drill species indigenous to Long Island Sound.

Materials and Methods

Collection of animals

The oyster drills, *U. cinerea* and *E. caudata,* were collected in Long Island Sound in the vicinity of the Norwalk Islands, Norwalk, Connecticut. This area is extensively used for farming oysters and is characterized by relatively shallow depths, moderate currents, and a variety of bottom substrata (sand, silt, gravel). It is also one of the few known areas on the Connecticut shore where relatively large numbers of both drill species can be obtained. During July and August 1967, when the majority of the drills were collected, the bottom salinities averaged 27‰ and the temperatures 22.2° C.

Two methods were employed for capturing the drills. The first consisted of setting drill traps in the relatively shallow water (3.6 m) off the southwest corner of Norwalk, town lot 19. The traps of chicken wire made into flat 64×30 cm bags were baited with 1-year-old oysters. At 2-week intervals the traps were retrieved, drills collected, and the traps freshly baited and reset.

Although this method provided approximately equal numbers of both drill species, it did not yield the large numbers of drills required. The second and more efficient method consisted of hand-picking drills from bottom material brought to the surface by standard oyster dredges. Norwalk town lots 35, 50, 80, and 207 were dredged by the oyster boat, "Cultivator" (Bloom Bros.), and the Bureau of Commercial Fisheries research vessel, "Shang Wheeler." This procedure proved to be a rapid and reliable means of drill collection.

Oyster spat (3–13 months old) were dredged from the same area. Some of the spat were from natural set (local and Fishers Island, New York) and some from commercial hatchery set (Bloom Bros., Stratford, Connecticut, and Vanderborgh-Radel, Oyster Bay, New York).

Conditioning

The drills were separated by species in the laboratory and placed in separate 60-liter fiberglass aquaria. The aquaria, arranged on a laboratory water table, were each supplied with a separate continuous flow of sea water at normal temperature (22.5° C) and salinity (26.5‰). Clusters of young oyster spat were added to each aquarium to provide food and substrate for the drills during the 1-week acclimatization period.

To condition the drills to the various salinity-temperature combinations, the sea water in which the drills were kept was gradually brought to the appropriate temperature and salinity. The temperature of the water entering the conditioning aquarium containing the drills to be exposed to a series of salinities at a particular temperature was either increased or decreased 1° C per day until the desired temperature was reached. The temperature was then held constant and the salinity was decreased by 1‰ per day until the desired salinity was reached.

As each salinity level was attained, groups of drills were removed from the conditioning aquaria and placed into a holding aquarium maintained at that temperature and salinity, until one holding aquarium was established at each of the four salinities to be tested. After 1 week in these holding aquaria and before the experiments the drills were live-sexed by the method described by Hargis (1957) and segregated by sex in separate aquaria. To insure that the drills were sexually mature, only females 20 mm or larger and males with a well-developed penis were used in the experiments.

Groups of 20 drills (14 females and 6 males) were then removed for use in the experimental trays. The remainder were kept in the holding aquarium throughout the experiment to supply conditioned drills to replace those that died during the experiment. All aquaria were drained and cleaned at 1-week intervals.

The young *C. virginica* used as prey were not conditioned; they were held in aquaria supplied with running water at normal temperature and salinity.

Experimental procedure

Each laboratory at the Milford Biological Laboratory of the Bureau of Commercial Fisheries is supplied with running hot and cold sea water, as well as cold fresh well water. By combining streams of water from these three sources a variety of temperatures and salinities can be obtained. An apparatus similar to the one described by Loosanoff (1949) and Loosanoff and Smith (1950) was used to maintain a flow of water at the desired temperature and salinity. The required combinations of temperature and salinity were obtained by adjusting the rate of flow from each of the three water sources to several polyethylene mixing cylinders placed above a laboratory water table. The flow of water to the cylinders was adjusted so that the surplus continuously drained through the overflows, thus keeping the water level and head pressure constant in all cylinders. A Y-tube at the outlet from each cylinder provided two separate streams of water which supplied two fiberglass trays (35 cm × 48 cm × 11.5 cm), each containing 20 oyster

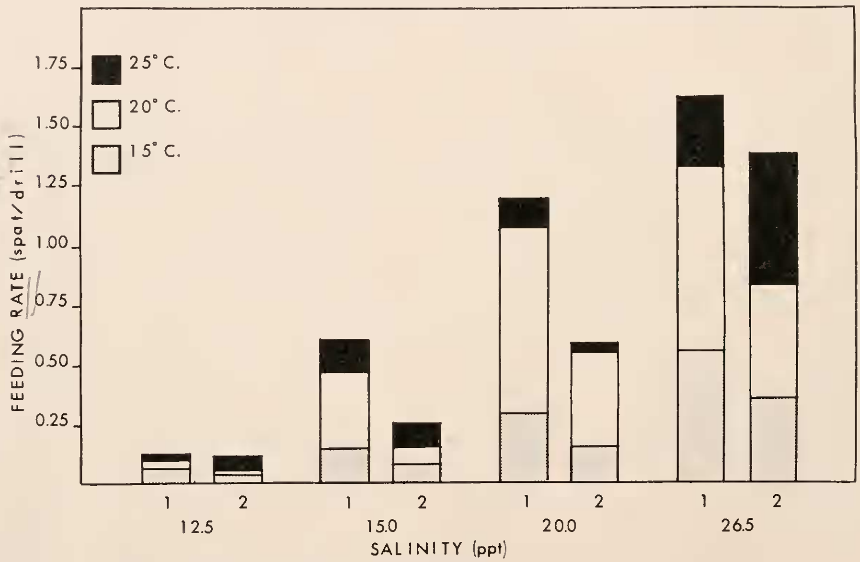

FIGURE 1. Feeding rates of *Urosalpinx cinerea* (1) and *Eupleura caudata* (2), per 10-day trial, on young *Crassostrea virginica*, at a series of controlled temperatures and salinities.

drills. The rate of flow to each tray was approximately 2 liters per minute. The trays were covered with small-mesh nylon netting to prevent the drills from escaping.

Three experiments were conducted to determine the combined effects of salinity and temperature on certain fundamental activities of *U. cinerea* and *E. caudata*. The same salinities (12.5, 15, 20, and 26.5 ± 1‰) were repeated in each experiment, but the temperature was different. Salinity was measured daily by hydrometers calibrated at 17.5° C and corrected for temperature with the hydrographical tables of Knudsen (1901). Each experiment consisted of five 10-day trials; thus, the total elapsed time was 150 days. The salinity tolerance of the drills was studied at temperatures of 15, 20, and 25 ± 1° C.

The four salinities used in each of the three experiments were established by the method previously described. Two trays were kept at each salinity; one contained 20 *U. cinerea* and the other, 20 *E. caudata*. Both trays were stocked with approximately 60 spat (*C. virginica*) on 5 to 6 clusters. The trays were examined daily and were drained, cleaned, and restocked at 10-day intervals. At the end of each 10-day trial the rates of feeding, ovipositing, and survival were determined. Consumed prey were distinguished from other prey mortalities by a simple criterion—the presence of a perforation through one of the valves. Dead drills were easily identified by the putrifying tissue usually observable in the shell aperture. Unusual podial extension or retraction, however, often indicated morbidity, and drills were tested for viability by pin-prick or exposure to water of normal temperature. Reproductive rates were measured by the numbers of egg capsules deposited during each 10-day trial. Counts of egg numbers in each capsule were also made. With this procedure both drill species were studied simultaneously in the presence of the same prey species at the salinities and temperatures established for each experiment.

Results and Discussion

Effects of salinity and temperature on feeding

Feeding rates at the 12 salinity-temperature combinations were recorded as the mean number of oyster spat consumed per drill per 10-day trial (Table I). At 15° C the feeding rates of both drill species increased from minimal (0.05 and 0.01) at a salinity of 12.5‰ to moderate (0.54 and 0.29) at 26.5‰. At the lower salinities (12.5 and 15‰) the drills remained relatively inactive, exhibiting little tendency to move toward or attack prey; however, they were firmly attached to the trays or shell clusters. As the salinity increased, general drill activity increased.

Feeding rates at 20° C were significantly higher at all salinities than at 15° C (Table I). At 12.5‰ the number of prey consumed per drill per trial was still

Table I

Feeding rates of Urosalpinx cinerea *and* Eupleura caudata *during five 10-day trials at a series of controlled water temperatures and salinities**

Drill species and salinity ‰	Average no. of prey consumed per trial			Average no. of prey consumed per drill per trial		
	Temperature °C			Temperature °C		
	15.0	20.0	25.0	15.0	20.0	25.0
U. cinerea						
12.5	1.0	1.8	2.0	0.05	0.09	0.10
15.0	2.8	9.4	10.6	0.14	0.47	0.53
20.0	5.4	21.0	23.2	0.27	1.05	1.16
26.5	10.8	26.0	33.2	0.54	1.30	1.66
E. caudata						
12.5	0.2	0.6	1.6	0.01	0.03	0.08
15.0	1.4	2.8	4.4	0.07	0.14	0.22
20.0	2.8	10.8	11.4	0.14	0.54	0.57
26.5	5.8	16.2	27.0	0.29	0.81	1.35

* In each trial 20 drills were held in a tray with approximately 60 *Crassostrea virginica* spat.

low (0.09 and 0.03) but the combined increase in feeding of both drill species with each increase in salinity was higher than it was at 15° C. At normal salinity (26.5‰) the feeding rates of both drills were relatively high (1.30 and 0.81).

At all salinities the drills held at 25° C showed the highest feeding rates (Table I). The rate of prey consumption increased from 0.10 and 0.08 oyster spat per drill per trial at 12.5‰ to the maximum observed rates of 1.66 and 1.35 at normal salinity (26.5‰). At no time during the experiment did the drills consume all the prey available; thus, availability of food did not limit feeding.

At each salinity the feeding rates of both species increased with each increase in temperature; also, at each temperature they increased with each increase in salinity. The increased feeding rates at high temperatures were expected (Hanks, 1957), but the increased feeding rates with each increase in salinity did not agree with the findings of Haskin (1935). He found that the rate of feeding was not appreciably altered within the salinity range of his study (10 to 25‰). Results of the present series of experiments do support Haskin's conclusion that feeding stops below 10–12‰, but they also indicate that the feeding rates of both species of drills are appreciably altered by salinity at all three temperatures studied. The feeding rates of both *U. cinerea* and *E. caudata* at normal salinity (26.5‰) at each temperature agreed with previous feeding rates established for *U. cinerea* (Hanks, 1957) and *E. caudata* (Manzi, in preparation).

A comparison of the feeding rates of the two drills showed that *U. cinerea* was consistently the more voracious oyster predator at all temperature-salinity combinations studied (Fig. 1). At the lower combinations *E. caudata* consumed young oyster spat at approximately one-third of the rate exhibited by *U. cinerea.* At the higher combinations, however, the disparity was considerably reduced. These observations indicate that *U. cinerea* is probably the more serious predator of *C. virginica;* it should not be inferred, however, that *U. cinerea* is the more voracious predator on other common prey of the two drills.

Both drill species were cannibalistic in many of the experimental trays. The rate of cannibalism increased as the feeding rates increased, and the highest incidence of cannibalism was at the optimum feeding conditions (25° C, 26.5‰). Although cannibalism has been observed in both drill species previously (Flower, 1954; C. L. MacKenzie, Jr., Bureau of Commercial Fisheries, Milford, Connecticut, personal communication), findings of the present study confirm my previous observations (Manzi, in preparation) of cannibalism throughout the limits of the drill's feeding range in the presence of alternative food sources. Both drill species were cannibalistic, but *E. caudata* was the more so, which may have had a significant bearing on the results observed. In all cases where active cannibalism was observed the predators were always female drills.

Statistical evaluation of the results by "t" tests revealed that the differences in feeding rates at the progressively increasing salinities were significant (95% confidence level, $t > 4.604$ with d.f. $= 4$), for each species of drill, at all temperature levels. At 12.5‰ salinity "t" tests showed no significant difference in feeding rates at temperatures of 15, 20, and 25° C. At all higher salinities, differences in feeding rates at the three different temperatures were significant at the 95% confidence level.

Effect of salinity and temperature on reproduction

Neither species of oyster drill deposited egg capsules at salinities of 15‰ or lower (Table II). At 20‰ *U. cinerea* did not deposit egg capsules at 15° C although *E. caudata* deposited a few (13). At higher temperatures both species of drills deposited egg capsules, and both species deposited more capsules at 25° C than at 20° C (Table II). At a salinity of 26.5‰ both drills deposited egg capsules at all temperatures tested (15, 20, and 25° C).

Within the range of temperature and salinity at which oviposition occurs, the number of capsules deposited by *E. caudata* and *U. cinerea* increased with each increase in temperature and salinity (Fig. 2). These results indicate that the

TABLE II

Reproductive rates of Urosalpinx cinerea *and* Eupleura caudata *during five 10-day trials at a series of controlled water temperatures and salinities**

Drill species and salinity ‰	Total no. of egg capsules deposited			Average no. of eggs per capsule		
	Temperature °C			Temperature °C		
	15.0	20.0	25.0	15.0	20.0	25.0
U. cinerea						
12.5	0	0	0	0	0	0
15.0	0	0	0	0	0	0
20.0	0	135	174	0	11.6	13.2
26.5	108	261	271	9.8	10.8	10.0
E. caudata						
12.5	0	0	0	0	0	0
15.0	0	0	0	0	0	0
20.0	13	21	108	18.6	17.8	20.4
26.5	33	158	312	19.4	18.8	19.6

* 20 drills (14 females and 6 males) were used in each trial.

effects of temperature and salinity on reproduction of oyster drills are interrelated, and confirm the conclusions of Haskin (1935) and Stauber (1943) that oyster drills can survive in areas where they cannot reproduce.

The reproductive rates of *U. cinerea* and *E. caudata* were not greatly different; *U. cinerea,* however, deposited slightly more egg capsules than *E. caudata* at most of the temperature-salinity combinations within the range at which oviposition occurred.

The number of eggs per capsule did not vary with temperature and salinity. The number of eggs per capsule differed significantly, however, between species. *U. cinerea* deposited an average of 11.1 eggs per capsule, with a range of means from 9.8 to 13.2 eggs per capsule (Table II), and *E. caudata* deposited almost twice as many, an average of 19.1 and a range from 17.8 to 20.4 eggs per capsule. The lack of variation in the number of ova per capsule for each drill species at the different temperature-salinity combinations could be due to an effect on production of either ripe ova or egg capsules. The increased reproductive rate

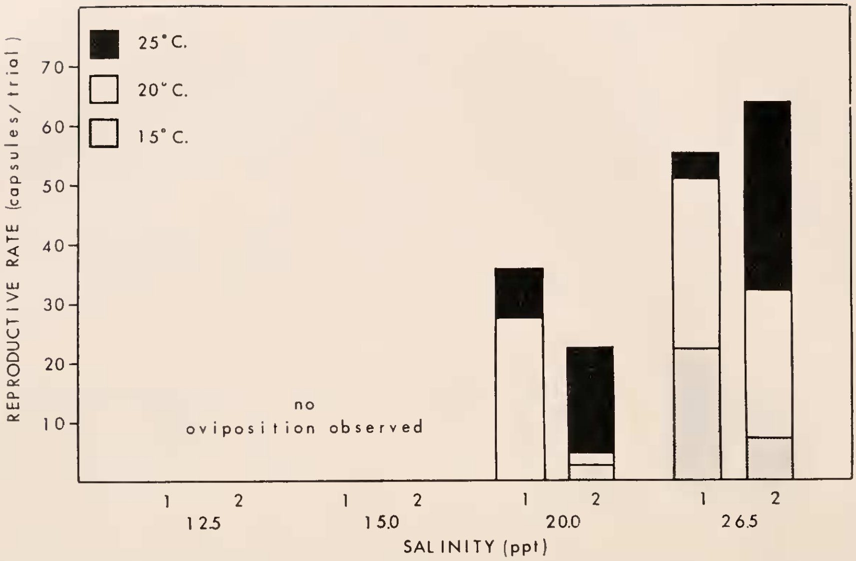

FIGURE 2. Reproductive rates of *Urosalpinx cinerea* (1) and *Eupleura caudata* (2), per 10-day trial, at a series of controlled temperatures and salinities.

at higher temperatures and salinities, however, may be the result of a generally increased metabolic rate affecting both ripening of ova and production of egg capsules.

Effects of salinity and temperature on survival

Drill mortalities were recorded as the mean number of drills dying during a 10-day trial, as well as the percentage mortality per trial (Table III). The lowest

TABLE III

Mortality rates of Urosalpinx cinerea *and* Eupleura caudata *during five 10-day trials at a series of controlled water temperatures and salinities*

Drill species and salinity ‰	Average no. of drill deaths per trial			Per cent drill mortality per trial		
	Temperature °C			Temperature °C		
	15.0	20.0	25.0	15.0	20.0	25.0
U. cinerea						
12.5	1.6	3.8	6.8	8	19	34
15.0	2.0	2.4	3.4	10	12	17
20.0	0.8	1.0	1.4	4	5	7
26.5	0.2	0.4	1.2	1	2	6
E. caudata						
12.5	2.2	4.0	8.2	11	20	41
15.0	3.0	3.6	4.4	15	18	22
20.0	0.8	1.0	2.4	4	5	12
26.5	0.4	0.6	1.4	2	3	7

death rate at each salinity was at 15° C. The highest mortalities of *U. cinerea* and *E. caudata* at this temperature occurred at 15‰ salinity (10 and 15%, respectively). At normal salinity and 15° C mortalities of the two species were lower (1 and 2%, respectively) than for any other temperature-salinity combination tested.

At 20° C and 12.5‰ salinity *U. cinerea* displayed 19% mortality and *E. caudata* 20%. Mortality at this temperature decreased with each increase in salinity and the lowest mortality at this temperature was at 26.5‰; *U. cinerea*, 2% and *E. caudata*, 3%.

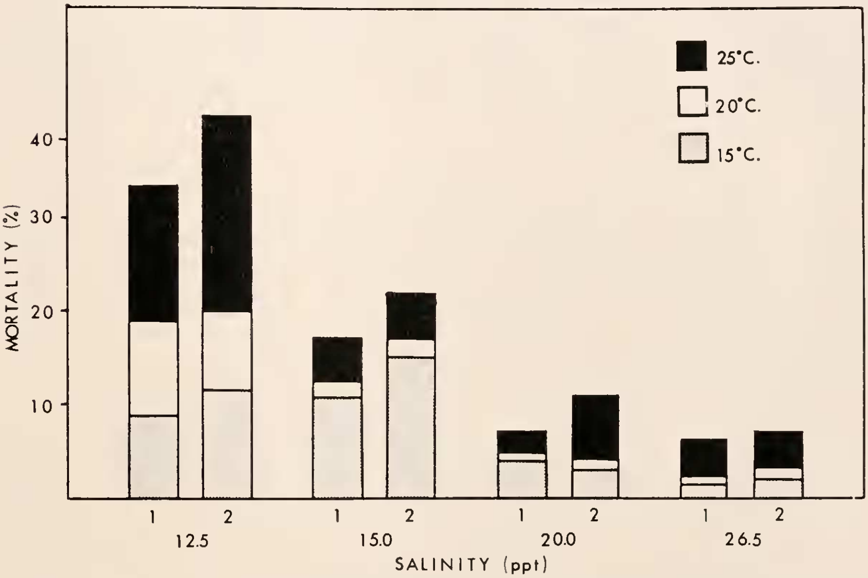

FIGURE 3. Mortalities of *Urosalpinx cinerea* (1) and *Eupleura caudata* (2) at a series of controlled temperatures and salinities.

The highest mortality at all salinities was at 25° C. At this temperature and 12.5‰ salinity, *U. cinerea* and *E. caudata* exhibited mortalities of 34 and 41%, respectively—higher than at any other temperature-salinity combination tested. Again, the mortalities decreased as the salinity increased, and the lowest mortality at this temperature was at 26.5‰.

The ability of oyster drills to survive, particularly at low salinities, was markedly affected by temperature. Both species of drills exhibited progressively higher mortalities as the temperature was increased at each salinity, and at 12.5‰ the mortality rates were approximately four times higher at 25° C than at 15° C (Fig. 3).

These observations may explain the survival of drills in areas where seasonal fluctuations in salinity are wide. In late winter and early spring, when the salinity of coastal waters is lowest, the water temperature is still low enough for drills to withstand the low salinities for some time. *E. caudata*, however, was less tolerant than *U. cinerea* to lower salinities at all temperatures studied; this feature could explain the absence of *E. caudata* in intertidal zones and other areas with wide fluctuations in salinity where *U. cinerea* is frequently found.

At the temperature-salinity combinations where feeding rates were moderate to high, cannibalism accounted for a relatively large part of the drill mortalities. At the high temperature-low salinity combinations, where the mortalities were highest, cannibalism was rare and did not significantly affect the mortalities recorded.

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Summary

1. At all temperatures studied the limited feeding of *Urosalpinx cinerea* and *Eupleura caudata* at 12.5‰ indicates that this salinity is near the lower limit for feeding.

2. The feeding rates increased with each increase in temperature and salinity.

3. The maximum feeding rates were at the highest temperature-salinity combination studied (25° C, 26.5‰).

4. At all temperature and salinity combinations *U. cinerea* consumed more oyster spat than did *E. caudata.* Given equal populations, therefore, *U. cinerea* is the more important of the two species as a predator of *Crassostrea virginica.*

5. Both species of drills exhibited cannibalism in the presence of alternative food sources, but *E. caudata* did so to a greater extent than *U. cinerea.*

6. Cannibalism increased as the feeding rate increased, and the highest incidence of cannibalism was at optimum feeding conditions.

7. In all instances of cannibalism the predators were female drills.

8. The mortality rates of both species of drills increased with increasing temperature and decreasing salinity.

9. Mortality was highest at the highest temperature and lowest salinity combination (25° C, 12.5‰) and lowest at the lowest temperature and highest salinity (15° C, 26.5‰).

10. *E. caudata* was less tolerant than *U. cinerea* to low salinities at all temperatures.

11. *E. caudata* began ovipositing at 15° C and 20‰, and *U. cinerea* at 20° C and 20‰.

12. The number of egg capsules deposited by each species of drill increased with each increase in temperature and salinity; the maximum number was deposited at 26.5‰ at all temperatures studied.

13. The number of eggs in each capsule did not appear to be affected by temperature or salinity.

LITERATURE CITED

ADAMS, J. R., 1947. The oyster drill in Canada. *Fish. Res. Board Can., Progr. Rept.*, **37**: 14–18.

CALABRESE, A., 1969. Individual and combined effects of salinity and temperature on embryos and larvae of the coot clam, *Mulinia lateralis* (Say). *Biol. Bull.*, **137**: 417–428.

CARRIKER, M. R., 1955. Critical review of the biology and control of oyster drills *Urosalpinx* and *Eupleura*. *U. S. Fish Wildlife Serv., Spec. Sci. Rept.*, **148**: 1–150.

COLE, H. A., 1942. The American whelk tingle, *Urosalpinx cinerea* (Say), on British oyster beds. *J. Mar. Biol. Ass. U. K.*, **25**: 477–508.

DAVIS, H. C., AND A. CALABRESE, 1964. Combined effects of temperature and salinity on development of eggs and growth of larvae of *M. mercenaria* and *C. virginica*. *Fish. Bull., U. S. Fish Wildlife Serv.*, **63**: 643–655.

FEDERIGHI, H., 1931a. Studies on the oyster drill (*Urosalpinx cinerea* Say.) *Bulletin U. S. Bureau of Fisheries*, **47**: 83–115.

FEDERIGHI, H., 1931b. Salinity death-points of the oyster drill snail, *Urosalpinx cinerea* Say. *Ecology*, **12**: 346–353.

FLOWER, F. B., 1954. A new enemy of the oyster drill. *Science*, **120**: 231–232.

FRANZ, D. R., 1966. Some studies on physiological variation among populations of the oyster drill, *Urosalpinx cinerea*. *Proc. Nat. Shellfish. Ass.*, **56**: 3.

FRANZ, D. R., 1967. Further studies on physiological variation among populations of oyster drills. *Proc. Nat. Shellfish. Ass.*, **57**: 2.

GALTSOFF, P. S., H. F. PRYTHERCH AND J. B. ENGLE, 1937. Natural history and methods of controlling the common oyster drills (*Urosalpinx cinerea* Say and *Eupleura caudata* (Say). *U. S. Bureau of Fisheries Circ.*, No. **25**: 1–24.

GRIFFITH, G. W., AND J. B. ENGLE, 1962. Role of salinity in the distribution of the oyster drill, *Urosalpinx cinerea*, in the Rappahannock River, Virginia. *Unpubl. Rept. U. S. Fish Wildlife Serv.*, Oxford, Maryland. (Available from Bureau of Commercial Fisheries Library, Milford, Connecticut).

HANCOCK, D. A., 1954. The destruction of oyster spat by *Urosalpinx cinerea* (Say) on Essex oyster beds. *J. Cons. Perm. Int. Explor. Mer.*, **20**: 186–196.

HANCOCK, D. A., 1959. The biology and control of the American whelk tingle *Urosalpinx cinerea* (Say) on English oyster beds. *Ministry of Agriculture, Fisheries and Food, Fishery Investigations, London, Series II*, **22**: 1–66.

HANKS, J. E., 1957. The rate of feeding of the common oyster drill, *Urosalpinx cinerea* (Say), at controlled water temperatures. *Biol. Bull.*, **112**: 330–335.

HARGIS, W. J., 1957. A rapid live-sexing technique for *Urosalpinx cinerea* and *Eupleura caudata*, with notes on previous methods. *Limnol. Oceanogr.*, **2**: 41–42.

HASKIN, H. H., 1935. Investigations into the boring and reproductive activities of the oyster drills *Urosalpinx cinerea* (Say) and *Eupleura* sp. *Unpubl. Rept. U. S. Bur. Fish.*, Washington, D. C. (Available from Bureau of Commercial Fisheries Library, Milford, Connecticut).

KINNE, O., 1964. The effects of temperature and salinity on marine and brackish water animals. II. Salinity and temperature-salinity combinations. *Oceanogr. Mar. Biol. Annu. Rev.*, **2**: 281–339.

KNUDSEN, M., 1901. *Hydrographical Tables*. Copenhagen, G. E. C. Gad. 1901. [2nd ed. 1931, pp. 1–63, photoprinted by Tutein and Koch.]

LOOSANOFF, V. L., 1949. Method for supplying a laboratory with warm sea water in winter. *Science*, **110**: 192–193.

LOOSANOFF, V. L., AND H. C. DAVIS, 1951. Behavior of drills of different geographical districts at the same temperature. *Unpubl. Rept. U. S. Fish Wildlife Serv.*, Milford. Conn. (Available from Bureau of Commercial Fisheries Library, Milford, Connecticut).

LOOSANOFF, V. L., AND P. B. SMITH, 1950. Apparatus for maintaining several streams of water of different constant salinities. *Ecology*, **31**: 473–474.

Nelson, J. R., 1931. Trapping the oyster drill. *Bulletin New Jersey Agricultural Experimental Station,* **583**: 1–12.

Sizer, I. W., 1936. Observations on the oyster drill with special reference to its movement and to the permeability of its egg case membrane. *Unpubl. Rept. U. S. Bur. Fish.,* Washington, D. C. (Available from Bureau of Commercial Fisheries Library, Milford, Connecticut).

Stauber, L. A., 1943. Ecological studies on the oyster drill, *Urosalpinx cinerea,* in Delaware Bay, with notes on the associated drill, *Eupleura caudata,* and with practical consideration of control methods. *Unpubl. Rept. Oyster Res. Lab.,* N. J. (Available from L. A. Stauber, Rutgers University, New Brunswick, New Jersey).

Stauber, L. A., 1950. The problem of physiological species with special reference to oysters and oyster drills. *Ecology,* **31**: 109–118.